

b. Node at which the first abnormality appeared.—Varieties showed a slight difference in the node at which the first compound leaf or whorl appeared. It was usually the second node in Ottawa 770B and Punjab, the third node in Walsh, and the second, fifth and sixth nodes in F257 (Table 5).

There was no marked difference between varieties in the ratio of seedlings affected at one and more than one node. The latter constituted 22%, 15%, 18% and 9% of the total number of affected seedlings in Ottawa 770B, Punjab, Walsh and F257 respectively. The low figure for F257 is scarcely significant considering the few plants affected (Table 6).

Multiple leaves occurred in all lines. There was no significant difference in the ratio of multiple to compound leaves between the varieties.

TABLE 6.
Number of Seedlings with Abnormalities at More than One Node.

	Ottawa 770B.	Punjab.	Walsh.	F257.
Number of seedlings with abnormalities	207	153	11	58
Number of seedlings with two affected nodes	40	20	2	5
Number of seedlings with three affected nodes	6	3	—	—
Percentage of seedlings with more than one affected node among abnormal seedlings	22	15	18	9

Abnormalities in Hybrid Populations.

The frequency of abnormalities in hybrids was no greater than in varieties, and was often surprisingly low, e.g. Williston Golden and Very Pale Blue Crimped hybrids. There were more in Ottawa 770B hybrids (Table 7), but even in the most affected cross, Ottawa 770B × Argentine F11, the number was well below the frequency in Ottawa 770B. The very low frequency in Ottawa 770B × Walsh may be the result of the dominance of the latter variety. The first abnormality tended to appear over a wider range of nodes in the Ottawa hybrids than in Ottawa itself, in which it usually appeared at the second node.

Effect of Abnormalities on Rust Reaction.

There was no detectable effect on the rust reaction. Ottawa 770B always gave normal reactions despite its high frequency of abnormalities. In Plate xvi, fig. 13, the reaction of a normal and compound leaf on the same seedling is seen to be identical.

TABLE 7.
Number of Seedlings with Abnormal Leaves in Hybrid Populations.

Date Sown.	Pedigree.	Total.	Number of Seedlings with First Abnormality at the Following Nodes.							
			2	3	4	5	6	7	8	9
16.5.52	(Ottawa × Argentine F11)	85/244	8	8	8	14	1		2	
	(Ottawa × Walsh) ..	29/234	6	2	6	10	5			
	(Ottawa × Morye) ..	48/249	4	8	15	16	1	3	1	1
	(Ottawa × Italia Roma) ..	46/251	8	15	3	11	3	4	1	1
	Total	26	33	32	51	10	7	4	2

Effect of the Environment.

Compound leaves and whorls occurred at most times of the year, but were less common in sowings made in the warmer months. A trial sowing of Ottawa 770B kept in the fluorescent-light rooms, with a moderately high and fairly constant temperature, was remarkably free from abnormalities, although growth was otherwise rather abnormal. Only one in 669 F257 seedlings had a compound leaf in sowings made between 1st February and 8th April, 1952. There was a marked increase in later sowings. Thirty of 123 Ottawa 770B seedlings sown 14th March and 8th April, 1952, and only 19 in 126 sown 1st April, 1953, had abnormal leaves. The frequency doubled in later sowings (Table 4).

Cones and typical fan off types, with two exceptions, appeared during midwinter, after periods of prolonged, and consistently low temperatures. Since they appeared simultaneously in the varieties affected, usually at the same node, in the open, under cold frames and in unheated glasshouses, temperature, rather than light intensity, degree of hardness of the seedling, etc., seems to be the responsible factor.

The Nature of the Cone Abnormalities.

Cones were always quadrate. The absence of the expected leaf pair at the next node, clearly demonstrated in affected F257 seedlings (Plate xvi, figs. 2, 4), confirmed the fact that two pairs of leaf primordia had become fused at the one node. There must therefore be a strong tendency for leaf primordia to associate in groups of two pairs prior to their separation by an internode. This is a fluid association which must readjust itself each time one of the pairs is removed from the primitive growing point by elongation of the internode. It is not an association of successive groups of four primordia, since this would preclude any association of the second and third, or fourth and fifth leaf pairs, realized at least once. It can also be inferred from the association of the first and second leaf pairs in the F257 cone abnormalities that no internode develops prior to germination.

Formation of the Leaf Abnormalities.

These abnormalities seem to be the product of a complex interaction between the variety, stage of seedling development and temperature, resulting finally in suppressed differentiation of primordia. In the cones, four leaf primordia have failed to separate, and developed as a solid crown of tissue with slight terminal separation of the primordia. Since the basic quadrate association of primordia is not disturbed, subsequent phyllotaxy is usually normal. The internode has been completely suppressed, but this has been compensated by longer internodes contiguous with the affected node.

In the leaf whorls the primordia have separated completely, but an internode has been suppressed.

Most of the compound leaves seem to be due to fusion or inadequate separation of contiguous primordia. The distortion of the quadrate association is reflected in the subsequently skewed phyllotaxy (Plate xvi, fig. 9; Text-figs. 15-19).

But some compound leaves must be due to over-differentiation. In a Walsh seedling with slight terminal bifurcation of one cotyledon, the two leaves immediately above in the same radius were similarly affected and must have resulted from the same process of over-differentiation (Text-fig. 22). The normal decussate phyllotaxy of the Ottawa 770B and Punjab seedlings (Text-figs. 20, 21) typical of many others is difficult to explain if the compound leaves are fused contiguous primordia. It is quite natural if they are bifurcated primordia, which would not affect the quadrate association of the original primordia.

STEM ABNORMALITIES.

At least 5% of out-of-season field-sown Concurrent F2 hybrids, Concurrent \times Ottawa 770B, Concurrent \times Tammes' Pale Blue and their reciprocals, were abnormal. The stems were fasciated, flat and ribbonny, for lengths upwards of a foot. The symptoms persisted into the inflorescence, usually reduced to a small club head, and produced bifurcated

flowers, fused anthers, filaments, styles and capsules. None of the F2 seedlings in crosses Punjab \times Koto, Punjab \times Ottawa, Punjab \times Tammes' Pale Blue and reciprocals, were abnormal.

There were three types of abnormalities among pot sown seedlings: (1) Fasciated epicotyl elongating without branching (Plate xvii, fig. 11); (2) Fasciated epicotyl branching into (a) a normal and fasciated shoot (Plate xvii, fig. 8), (b) two fasciated shoots (Plate xvii, fig. 13a), (c) two normal shoots (Plate xvii, fig. 12); and (3) Shoot branching into two normal shoots without any obvious prior fasciation (Plate xvii, figs. 9, 14).

The phyllotaxy, particularly in type 1 and 2 abnormalities, was most irregular. The leaves of the first two groups were often unusual compound forms. Multiple leaf clusters were common just below the point of bifurcation of type 3 seedlings. Primary shoots were usually affected, but each type also occurred on side shoots.

Mechanical Induction of Fasciation and Bifurcation.

The growing point and all the lateral buds of eight seedlings were damaged or destroyed by a grub. These, without exception, after a period of suppressed growth under optimal growing conditions, gave rise to very abnormal fasciated and bifurcated shoots with unusual compound leaves. Only one abnormal shoot was detected on twelve partially damaged seedlings, with several buds left intact.

Bifurcation and fasciation may thus result from suturing, or mechanical injury of meristematic tissue. In the absence of a normal, undamaged bud, the sutured tissue yields to the growth pressure and develops abnormal shoots. These conditions may well obtain in young seedlings, in which the growing point must be rather exposed to damage. If damaged by internal or external forces, growth continues along the only active axis then available and an abnormal shoot develops. At a later stage the growing point should be better protected, while other growing points could resume growth if the main shoot were damaged.

Pedigree of abnormal seedlings.

Type 1.—F391 \times Newland.

Type 2.—(Ottawa 770B \times Walsh) \times F257, (Ottawa 770B \times Kenya) \times F257, (Ottawa 770B \times Bison) \times F257, (Argentine F11 \times Abyssinian) \times F257, (Bison \times Kenya) \times F257, (Bolley Golden \times Newland) \times F257, (Bolley Golden \times Koto) \times F257, (Argentine F11 \times Newland) \times F257, (Tammes' Pale Blue \times Abyssinian) \times F257, Newland \times Akmolinsk, Ottawa 770B, Akmolinsk.

Type 3.—(Ottawa 770B \times Bison) \times F257, (Argentine F11 \times Ottawa 770B) \times F257, Akmolinsk \times Abyssinian, Kenya \times Abyssinian, Punjab \times Concurrent, Very Pale Blue Crimped.

CHLOROPHYLL DEFICIENCIES.

(Ottawa 770B \times Walsh) \times F257 (Plate xvii, fig. 6; Plate xvi, fig. 3).—The first symptoms appeared in a leaf at the third node of the primary shoot. Most of the subsequent leaves were affected, and the shoot finally died. The deficient tissue radiated from the leaf base in broken and unbroken lines of varying width. None of the secondary shoots were affected.

(Walsh \times Bison) \times F257 (Plate xvii, fig. 5).—The symptoms commenced about 12" up the stem of a secondary shoot. The chlorotic sectors were more clearly defined than the above specimen, and generally radiated from the base in a single strip. Fewer leaves were affected, and the symptoms persisted into the inflorescence. They were finally restricted to a small branch of the inflorescence, which failed to set seed. None of the other shoots were affected.

(Bison \times Kenya) \times F257 (Plate xvii, fig. 1).—A cotyledon deficiency, which did not persist into the shoot. The deficient sectors were confined to two thin lateral strips identically placed on both cotyledons.

A specimen of unknown pedigree (Plate xvii, fig. 2) showed an interesting medial band of deficient tissue on both cotyledons and the first leaf pair. The other leaves were normal.

MISCELLANEOUS ABNORMALITIES.

Divided Hypocotyl.

(*Argentine F11* × *Bison*) × *F257* (Plate xvii, fig. 17).—The hypocotyl had split medially along an axis at right angles to the cotyledons. The two leaves at the cotyledon node were missing. There seemed to be a minute epicotyl at the base of the cleft but it failed to develop. The root was also bifurcated.

An Aquatic Bud.

(*Ottawa 770B* × *Bison*) × *F257* (Plate xvii, fig. 14).—This seedling developed a type 3 bifurcated shoot, which was excised, and left in an almost full, $\frac{3}{4}$ -pint cream-jar in a moderately lighted section of a glasshouse. After about three weeks, a very unusual bud was noticed below the surface, just beneath the point of bifurcation. It had thick, very closely appressed, bract-like green leaves, and was much larger than normal. Despite careful efforts to maintain it, the bud failed to develop further.

Young buds, and occasionally young shoots grow aquatically, if left in well aerated vessels. But nothing like the above bud has ever developed.

TABLE 8.

Approximate Frequency of Abnormalities in F2, Double Cross and Varieties.

Type of Abnormality.	F2.	Double Crosses.	Varieties.
Polyembryos	1/3,000	9/6,000 ¹	2/3,000
Cotyledon abnormalities	21/5,000	11/5,000	3/6,000
Fasciation and bifurcation of the stem	8/5,000	10/5,000	3/6,000
Chlorophyll deficiencies	0/5,000	3/5,000	0/6,000
Compound leaves, etc.	No more frequent in hybrids than varieties.		

¹ Three of these were found in the crosses (*Ottawa 770B* × *Bison*) × *F257* and reciprocal, among about 150 seeds. This very high frequency was the only indication of specific genetic control of the abnormality. But 200 seeds from one pair were quite normal.

Bifurcated Basal Leaves and Growing Point.

(*Akmolinsk* × *Abyssinian*) × *F257* (Plate xvii, figs. 9, 10).—A single anticlinal suture seemed to have completely split the first two leaves medially, partially split the internode along the same axis, and produced two normal shoots, each carrying one of the two leaves normally expected at the second node. The medial splitting of the growing point is reflected in the spiral single leaf phyllotaxy of the derived shoots.

Fusion of Leaves at Different Nodes.

Two leaves at contiguous nodes were fused together medially, along their lateral margins (Plate xvi, fig. 15).

Bifurcation of a Leaf in Two Planes.

(*Walsh* × *Koto*) × *F257*.—The compound leaf consisted of two identical units fused together along the midrib. Each unit was slightly bifurcated distally.

Leaf-like sectors of tissue were appressed to the outer surface of some of the cone and fan type abnormalities noted in *F257* seedlings in 1951, but this was the only occurrence of such a kind.

DISCUSSION.

With the exception of the leaf abnormalities, all the aberrant types have either been confined to or been more frequent in hybrid lines than varieties (Table 8). There must, therefore, be some genetic factor operating with other external or internal forces initiating these abnormalities. They are either the product of some genetic complex occasionally realized in hybrid populations, or result from genetic imbalance.

There is not much evidence for the former. No one variety seemed to have a greater frequency of hybrid abnormalities than any other (but see footnote, Table 8), and progeny of several abnormalities, carried on to maturity, were normal.

The theory of genetic imbalance is more probable. The hybrids were derived from Flor's series of rust differential varieties, selected for their morphological and physiological diversity. Three of the major types of abnormality, polyembryony, cotyledon abnormalities, and fasciated epicotyls, and at least some of the fourth major group, leaf abnormalities, are probably produced by a common process, rather than unrelated processes. There seems to have been a proliferation of meristematic tissue, resulting in an enlarged growing face. The tissue has bifurcated and produced a double primordial complex, which has either continued development as a single fused unit, or separated into two normal and distinct primordia. This separation may occur early or late in development, and probably depends upon prior suturing of the complex. Several abnormalities have resulted from suturing without prior over-differentiation.

This process of over-differentiation, bifurcation and separation occurs from the earliest embryonic period to the late seedling stage, producing successively, polyembryos, split hypocotyledon, bifurcated cotyledons, fasciated and bifurcated epicotyls, and some bifurcated leaves.

The effect is generally localized to a single primordial segment, but may be more extensive, affecting simultaneously cotyledon and leaf type or phyllotaxy, leaf, internode and growing point, etc.

The compound leaves, cones, and whorls are a different phenomenon, resulting from suppressed separation of leaf primordia, and, by contrast with the other abnormalities, are as frequent in varieties as hybrids.

CONCLUSION.

Linum usitatissimum L. seems prone to a wide range of abnormalities. The major types seem to be an expression of genetic imbalance in hybrid populations, with internal stresses resulting in over-differentiation and bifurcation of meristematic tissue. Some of the most common abnormalities, compound leaves, seem to derive from this process. But many compound leaves are the end-product of a distinctly different process, suppressed separation of leaf primordia.

Acknowledgements.

This work was done during tenure of a Thomas Lawrance Pawlett Scholarship at Sydney University. I am deeply indebted to Professor W. L. Waterhouse for his unflinching encouragement and advice, particularly in compiling the photographic records.

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EXPLANATION OF PLATES XVI-XVII.

Plate xvi.

1. Seedling with fan and cone type abnormalities. $\times 1.3$.
2. *a, b*, Seedlings with cones at the first node and short internode below; second leaf pair at right angles to cotyledons. *c*, Normal F257 seedling with second leaf pair in same radius as cotyledons. $\times 1$.
3. Chlorophyll deficient primary shoot. $\times 0.7$.
4. *a, c*, Seedlings (F257) with cones at node 1. Note longer internode above and obvious lack of a leaf pair. *b*, Normal seedling. $\times 0.6$.
5. A cone slightly sutured from the base. $\times 1.8$.
6. *a*, Undeveloped cone at node 1. *b*, Expanded cone showing quadrate structure. *c*, Normal seedling. $\times 1$.

7. Seedling with fan showing rather long contiguous internodes. $\times 0.5$
8. Seedling with cone showing rather long contiguous internodes. $\times 0.5$
9. Abnormal seedling showing skewed phyllotaxy following fusion of contiguous leaf primordia. $\times 1.7$
10. Compound leaf with slight terminal differentiation at same node with a normal leaf. Note bifurcated leaf at next node. $\times 1.4$
11. An everted cone. $\times 1.6$
12. Compound and normal leaf at same node, showing varying degrees of separation of subleaves. $\times 1.4$
13. Identical susceptible rust reactions on normal and compound leaves. $\times 1.7$
14. Polyembryo with two roots emerging from germinating seed. $\times 1$
15. Fusion of two leaves at contiguous nodes. $\times 1.6$

Plate xvii.

1. Chlorophyll deficient cotyledons with lateral strips of completely deficient tissue. $\times 2.1$
2. Chlorophyll deficient cotyledons and first leaf pair with medial and distal deficient sectors. $\times 1.3$
3. Type 2 cotyledon abnormality with four subcotyledons. $\times 1.6$.
4. A side view of the same abnormality. $\times 1.4$.
5. Chlorophyll-deficient leaves from a side shoot, showing clearly defined radial deficient sectors. $\times 1.1$
6. Chlorophyll-deficient leaves with radial sectors of varying intensity and size (see also Plate xvi, fig. 3). $\times 0.8$.
7. A seedling with an extra cotyledon separated from the two normal cotyledons by a short internode. $\times 1.2$
8. A fasciated shoot bifurcating into a normal and fasciated shoot. Note the abnormal leaves. $\times 1.1$
9. A seedling, in which the epicotyl has been split medially without prior fasciation. The bottom internode has been partially sutured separating the two leaves at the second node, which now appear separately at the same level, still oppositely placed on the derived shoots. $\times 0.7$.
10. The same seedling with the two basal leaves split medially. $\times 1.6$.
11. A type 1 fasciated shoot, elongating without bifurcation. $\times 0.7$.
12. Two fasciated side shoots from the same seedling with one branching into two normal shoots. $\times 0.5$.
13. A fasciated seedling showing various types of branching, (a) into two fasciated shoots, (b) into a normal and fasciated shoot. $\times 0.6$.
14. An aquatic bud, with large, bract-like leaves, observed just below the point of bifurcation of the primary shoot. Note the small normal bud at the base of the shoot. $\times 1.2$.
15. a, An abnormal seedling with a whorl of three cotyledons and three leaves. b, An abnormal seedling with three cotyledons, two of which are closely appressed together and seem to have been derived by suturing of one of the two original cotyledon primordia. Note only two leaves at the bottom node. $\times 1.1$.
16. a, Slight terminal bifurcation of a cotyledon. b, A normal pair of cotyledons. $\times 1.1$.
17. An abnormal seedling with a split hypocotyledon. $\times 1.8$.
18. A seedling with three cotyledons, and three basal leaves. One cotyledon is much smaller than the other two. $\times 1.4$.

NOTES ON AUSTRALIAN THYNNINAE.

I. ARIPHRON BICOLOR ERICHSON.

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(Communicated by Dr. A. J. Nicholson.)

(Fifteen Text-figures.)

[Read 25th November, 1953.]

Synopsis.

Basic references to the species and its synonymy are given, followed by a concise description of both sexes, with the distribution range and flight period. The life-cycle is outlined as far as known, and the second instar larva and cocoon are described. The first instar larval characters are also described as far as possible from the exuvium. The more important adult and pre-adult features are illustrated by line drawings.

This paper will introduce a series of short descriptive notes on the Thynninae of Australia, with particular emphasis on the figuring of species concerned. The keys of Turner (1907, 1908, 1910) cannot be interpreted, and the bulk of his specific and generic descriptions are extremely difficult to follow, largely on account of lack of illustration of characters described. Consequently it is felt that emphasis should now be placed on clear figuring of the more important characters, with a minimum of word description.

Only species of certain identity will be described in this series of papers and, where possible, information on host records, flight periods, general habits and distribution will be included.

ARIPHRON BICOLOR ERICHSON, 1842.

Arch. f. Naturgesch. Berlin, 8:264 (♀).—*rigidulus* Turner, 1907, *Proc. Linn. Soc. N.S.W.*, 32:274 (♀); 1913, *Proc. Linn. Soc. N.S.W.*, 38:610 (synonymy).

♂.—Colour remarkably constant in the four specimens examined, and very distinctive for the species. Black; antennae, palpi, legs except for coxae and trochanters, abdomen except for segments 5, 4 and posterior portion of 3, and tegulae, rufo-testaceous. Wings very slightly fumose, with darker areas below and distad of stigma.

Gross structure as in Text-figures 1, 3, 4, and 10. Note particularly area "a" in Text-figure 4, which is smooth and without vestiture. The presence of this area is characteristic of Australian members of the tribe Thynnini, and its shape is in many cases highly diagnostic of genera and species.

Coarse rugose puncturing on most of vertex and frons including supra-antennal prominence, much finer on clypeus and genae. Vestiture of head sparse except for clypeus which is clothed with decumbent grey hairs. Thorax rather sparsely and irregularly punctured; abdomen almost impunctate.

♀.—Head, thorax, legs and terminal abdominal segments ferruginous; remainder of abdomen and eyes darker red-brown to black.

Gross structure as in Text-figures 2, and 5-9. Note particularly basal prominence on head, pronotal depressions, form of mesopleurae, and flange-structures of abdominal terminalia.

Coarse puncturing on frons and anterior part of vertex, fine, sparse puncturing on thorax, obsolete sculpture on abdomen. No rugosity or carinae on abdominal segments.

Material examined.—2 males, 1 female from Cavendish, Victoria; 2 males, 1 female from East Warburton, Victoria, Coll. F. E. Wilson.

Flight period.—January, February.

Distribution.—Tasmania and Southern Victoria.

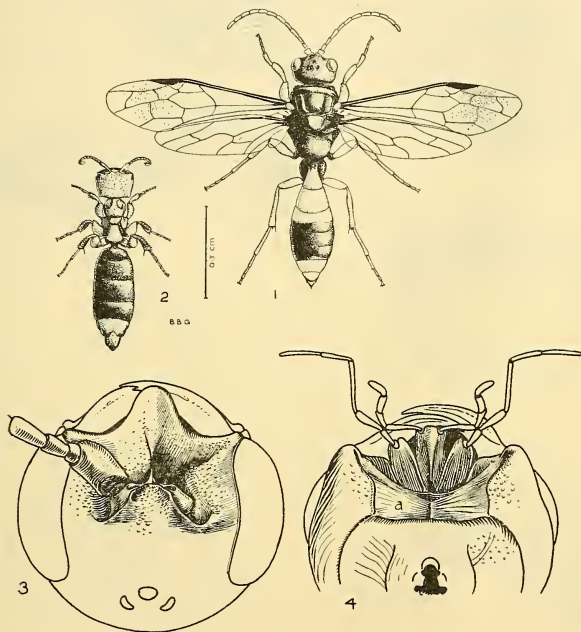
Note.—The subspecies *propodalis* Rohwer has not been seen by the writer.

Life cycle of Ariphton bicolor Erichs.

The entire life-cycle of this thynnid is not known, but the following remarks summarize information so far obtained.

Turner (1913, p. 610) makes the following remarks: "I took several males at Eaglehawk Neck in Tasmania, flying round and settling on a fallen Eucalyptus log, which contained a nest of *Myrmecia* ants. I searched the ants' nest as far as possible hoping to find the female, but was not successful."

Early in 1952, Mr. F. E. Wilson of Melbourne noted parallel occurrences at East Warburton, and succeeded in taking one male and a copulating pair.



Text-figs. 1-4.—*Ariphton bicolor* Erichs.

1, entire ♂; 2, entire ♀; 3, head, anterodorsal, ♂; 4, head, ventral, ♀.

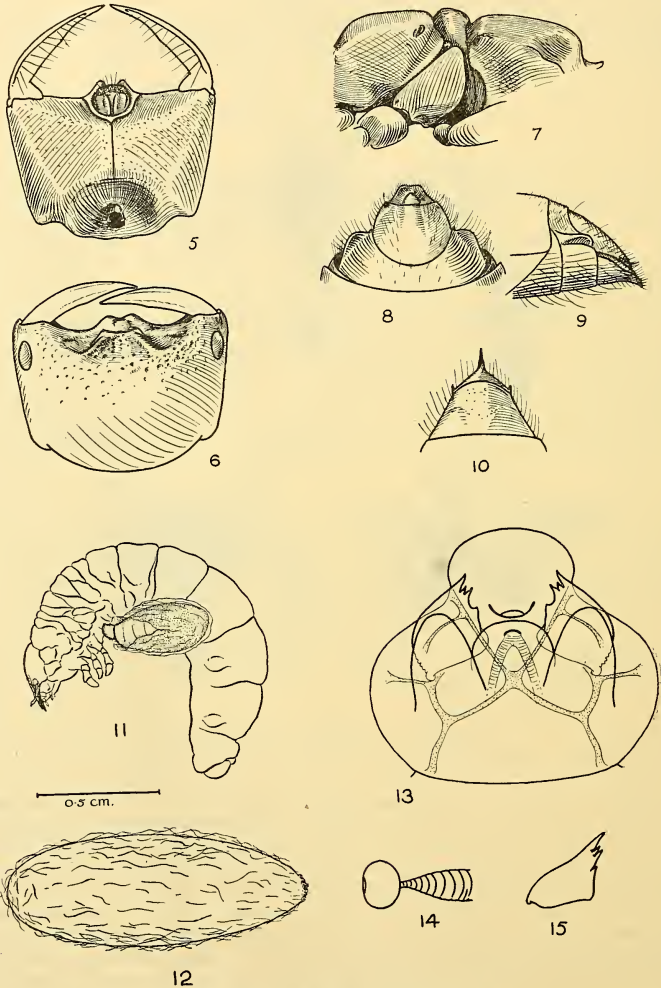
In January 1947, the writer made similar observations at Cavendish in Western Victoria, and on visiting the same log in January 1948, found males again ranging over it. On this occasion the log was split with an axe, and larvae and adults of a lucanid beetle were taken. The adults were identified by Mr. F. E. Wilson as *Syndesus cornutus* Fabr. One larva was found to have a second instar hymenopterous larva attached to its ventral surface, and a hymenopterous cocoon was taken, with the head-capsule of a lucanid larva loosely attached to its outer fibres. In another section of the log, an *Ariphton bicolor* female was found in a tunnel also containing a *Syndesus* larva, on the ventral surface of which was a typical thynnid egg. On this evidence it is assumed that the larva and cocoon herein described and figured, are those of *Ariphton bicolor*, and that a host of this thynnid is the lucanid *Syndesus cornutus* Fabr.

It is unfortunate that no final instar larvae of the parasite were collected, the only larva taken being in its second instar.

Description of second instar larva and cocoon of Ariphton bicolor.

The second instar larva is illustrated feeding on its host in Text-figure 11. The loose envelope covering the larva is the first instar cast skin.

The head capsule is well formed and sub-spherical, with powerful, toothed mandibles. No traces of antennae or palpi were detectable in slide mounts of the stained capsule.



Text-figs. 5-15.—*Ariphton bicolor* Erichs.

5, head, ventral, ♀; 6, head, dorsal, ♀; 7, thorax, lateral, ♀; 8, abdominal terminalia, dorsal, ♀; 9, abdominal terminalia, lateral, ♀; 10, abdominal terminalia, dorsal, ♂; 11, larval instar 2 on host; 12, cocoon; 13, larval instar 2, head, ventral; 14, larval instar 2, spiracle; 15, larval instar 1, mandible.

and no traces of vestiture or sculpture were noted on any portion of the body. The tentorium is of somewhat complex structure, and is illustrated by stippling in Text-figure 13. Oral lobes possibly representing labrum, labium and maxillae are well developed, and buccal and salivary openings are well defined.

Spiracles are all similar, and as illustrated in Text-figure 14.

The cocoon (Text-figure 12) is typical of the subfamily, consisting of a thin inner envelope, a compact, extremely tough, fine-textured main envelope, and an outer layer of fine, loose fibres. At the narrower (posterior) end is a small somewhat absorbent pad, which was in close contact with the tunnel wall. This pad, which evidently consists partly of larval faeces and is the only markedly water-absorbent part of the cocoon, appears to play a part in the moisture-conditioning of the cocoon interior.

The first instar larva.

The first instar skin was mounted and a mandible is illustrated in Text-figure 15. First instar spiracles are identical with those of second instar, except for size.

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